A SECOND MONOGRAPH OF THE GENUS *TISIPHONE*, HUBNER.

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Plates xxv., xxvi.

Introduction.

About fifteen years ago, I recognised that the butterfly, known as *Tisiphone abeona* Donovan, was one that was specially worthy of study. I then began an investigation on this species and its geographical races, which has continued almost without interruption ever since. This investigation has already borne important results and it is even now far from completed, but sufficient has been achieved to show that with this species the research undertaken has not been in vain and more important problems are clearly indicated. I have already published several papers dealing with this genus (23-29).

The species and its races are always eagerly sought for by collectors in other parts of the world, and they are always spoken of as some of the most handsome Satyrids of the world.

Historical.

The first mention of this species occurs in the first work devoted to Australian Insects (7), when Donovan in 1805 described and figured the upper and underside of a female of *"Papilio abeona."* He says: "There are few insects more striking than *Papilio abeona*. This appears to be one of the more common species of the Butterfly tribe in many parts of the Australasian regions; we receive it in this country not very infrequently among other insects from vicinity of the English Settlements at Port Jackson."

"It excites some surprise with us that, although a painting of this fine insect existed among the drawings of our worthy friend, William Jones, Esq., of Chelsea, at the time Fabricius was in this country, he should either by accident or design have omitted mentioning it, since he had unreserved access to these drawings and was indebted solely to them for his descriptions of nearly all the new species of the *Papilio* genus included in his 'Species Insectorum' (1781) and 'Entomologia Systematica' (1792-4)."

Even at the present time *abeona* can be found within a few miles of the centre of Sydney, and in the early days of the settlement here, must have been very common, where the busiest part of Sydney now stands. No doubt if Captain Cook had landed on the northern rather than the southern shore of Botany Bay, this species would have been caught by Sir Joseph Banks in 1770.

Hübner (10) under the name *Oreas marmorea zelinde* figured the upper and underside of a male, which is undoubtedly *abeona* and the race found at Sydney, though no locality was given. The generic name *Tisiphone* was first used by Hübner (11) in his catalogue, with *zelinde* (= *abeona*) as the first species. Scudder (20, p. 285) has shown that *abeona* must be taken as the type of *Tisiphone*, since Hübner's later use of *Tisiphone* for *hercyna* (a species from Mexico

to Brazil) in the second volume of his Exotic Butterflies, was much later than his Catalogue. (Scudder, 20, p. 96 and p. 285).

Godart (9) described both sexes and Boisduval (2) gave a short description under the name *Satyrus abeona* from New Holland.

From 1850 until the end of the century, various different genera were used. Westwood (30) placed *abeona* in *Lasiommata* section *Xenica*, the firstmentioned species being *acantha* Donovan, which by subsequent action became the type of *Xenica* (Scudder, 20, p. 289). Butler when describing (3) and figuring (4) his new species *joanna* used the genus *Enodia*, but almost immediately transferred (5, 6) *abeona* and *joanna* to *Xenica*, incorrectly designating *abeona* as the type. Semper (21) later also places *abeona* under *Xenica*.

Kirby (12) was the first to place the species in *Epinephile* and in this he was followed by Miskin (15, 16), Mathew (14), Staundinger (22), Olliff (17, 18), and Anderson and Spry (1). Miskin used this genus when describing the dark northern race *rawnsleyi* (15).

When I first began to collect butterflies, in 1893, *Epinephile* was in general use in Australia for these species, but when I published my Catalogue (23), 1903, I decided that Scudder's opinion (20) should be followed. I was unaware that Kirby (13) about the same time was taking similar action, as he proposed a new name *Manataria* for the American species included in *Tisiphone* and insisted that this name should be kept for *abeona* and its allies. This action has been followed ever since, except in the case of Seitz Macrolepidoptera, where in the American section Weymer still uses *Tisiphone* for *hercyna*. Fruhstorfer (8), however, in the Indo-Australian section points out that this usage is incorrect and insists that *Tisiphone* should be reserved for *abeona* and its allies.

The only other genus in which *abeona* has been placed is *Heteronympha* (type *merope*) in a paper by Wallengren which I have not been able to consult.

That *zelinde* is the same species as *abeona* is given by all the authors quoted who mention *zelinde*.

In 1903, in my Catalogue (23), I considered *abeona* and *joanna* as distinct species with *rawnsleyi* as a variety (what I considered *joanna* at that time was the race I subsequently described as *morrisi* (25)). This probably misled Fruhstorfer in his treatment of the genus in Seitz Macrolepidoptera (8) in which he gives *rawnsleyi* as a colour aberration and *joanna* as a race of *abeona*. In 1904 I separated the Victorian race, *albifascia* (24), in 1914 I described the white banded race *morrisi* (25), and in 1915 I separated another orange banded race *aurelia* (26), and in this paper I describe still another white banded race *regalis*.

The Systematic Position of the Species.

On account of the rudimentary nature of the front legs in both sexes, the swollen bases to three of the four principal veins in the fore-wing (Text-figure 1) and the closed cells in both wings in the imago, the almost smooth larva, the smooth pupa suspended by the tail, *Tisiphone abeona* is a typical Satyrid. It and *T. helena* the other species of the genus have no great affinity to the other Australian Satyrids, but rather stand alone.

Tisiphone helena from North Queensland bears a strong superficial resemblance to some species of the Amathusid genus *Morphopsis* from New Guinea. These species are about twice its size and when analysed marking by marking show a very close approximation to *T. helena*, but they lack the subtornal ocellus and the swollen veins of the forewing. I have little doubt that when the mountain fauna of that large island north of Australia is thoroughly investigated, a Satyrid allied to *Tisiphone* will be discovered.

Life History and Habits.

I have had all the stages of the seven races of *abeona* at one time and another, and cannot find any material differences in the early stages in any of them, so I treat them all together. Mr. F. P. Dodd tells me that he has bred *T. helena* at Kuranda, North Queensland, and from his remarks the larvae and pupae differ but slightly, if at all, from the corresponding stages of *T. abeona*.

a. *The Foodplant.*

All the races feed on species of *Gahnia*, a sedge-like plant commonly known as sword grass or cutty grass on account of the serrated edge to the leaves, and the hands invariably are cut when searching the plant for larvae or pupae. The plant on germinating from the seed sends up a single main shoot and later on from the base of this shoot many lateral shoots arise, and the plant increases in size to a large clump, often several feet round. It is found usually growing in moist situations, as in and around the coastal swamps where it sometimes almost completely covers an area of several acres. When the country is hilly it usually occurs in or close to the creek beds. This is usually its method of occurrence on mountains, though both in the Blue Mountains and the range west of Mackay I have found it growing quite away from water. It prefers sandy soil and grows to perfection in this soil when well drained, but if it gets a foothold in unfavourable situations it does not die out, for I have even found it growing on the Wianamatta Shale. In the early spring it sends up from the centre of the older shoots a long flowering spike and many young lateral shoots from the base. After many attempts at various times of the year, I have found that the spring is the best time to remove it into the experimental cages and ensure it growing.

Gahnia belongs to the *Cyperaceae*, a natural order of monocotyledonous plants. It is also the foodplant of many species of *Hesperiidae*. All the known larvae of Australian *Satyridae* feed on monocotyledonous plants and also all known larvae of the true Australian *Hesperiidae*, the exceptions in the latter family being the *Ismeninae* and *Hesperiinae*.

Gahnia psittacorum Labill. is the species that has the widest range, extending from Queensland through New South Wales and Victoria to Tasmania, and it is upon this species that the larvae of *Tisiphone* are most often found. It occupies large areas along the coast of eastern Australia, preferring the swamps, but also extends to an elevation of 4,000 ft. *G. aspera* Spreng., which does not favour such moist situations and is found usually at an altitude, is another species eaten by the larvae, and I have found them on a few occasions on *G. microstachya* Benth., a species occurring only above 2,000 ft. Probably all the species of *Gahnia* found within the range of *Tisiphone* are eaten by the larvae, but some of the species are rare. The correct determination of the species of *Gahnia* is admitted by botanists to be difficult.

Cladium jamaicense Crantz (*C. mariscus* R. Brown) has been recorded by Mathew (14) as the foodplant. This is not a common plant and, though *Tisiphone* probably does feed upon it, *Cladium* is not likely to occur in the locality given by Mathew.

I have never been able to get the larvae of *Tisiphone* to feed on any plant other than *Gahnia*, though the other Australian Satyrids will eat any soft grass and I have even found them feeding on *Gahnia*.

b. *The Egg.* (Plate xxv.).

The egg is nearly spherical, slightly flattened at the point of attachment, smooth to the eye, but when examined under a lens, is seen to be slightly roughened: it is without any fine vertical ribs as is usual in the eggs of many Satyrids. In colour it is yellow green, emerald green and rarely with a bluish tint. In size it is very large, exceeding in size the egg of *Papilio aegeus*, a butterfly over twice its wing expanse. The diameter of the egg is about twice that of the egg of *Heteronympha merope*, a species but little its inferior in size. The eggs are usually laid singly on the very young leaves of the foodplant that rise vertically from near the centre of a shoot; at times I have seen them laid either on the upper or under surface of the older leaves that had drooped over. On one occasion I saw an egg laid by a wild female on a dead twig near the foodplant. In the experimental cages they are sometimes laid on the sides of the cage, and once I found an egg attached to the leg of the parent.

When about to lay an egg the female alights on a leaf to which she clings with her four feet, she then places the end of her abdomen round the edge of the leaf so that it is touching the opposite side of the leaf to that on which she is resting. She then moves her abdomen slightly to seek a favourable spot to deposit the egg, and then places the end of the abdomen firmly against the leaf. The egg is then slightly obtruded, a short pause then occurs to allow the egg to adhere to the leaf and the abdomen is then slowly drawn away. In some cases another egg is laid near the first, but this is not always so, though usually two eggs are laid with a short interval between, the female then flying away and waiting some considerable time before laying further eggs. The number of eggs laid by one female has varied from 16 to 58, though more than 40 is very unusual. In four cases only were all the eggs contained in the abdomen deposited. In my experimental work it has been my custom to dissect the remaining eggs from the abdomen whenever I consider it necessary to kill the female. From 39 records kept the average number of eggs laid was 25; and from 26 completed records the average number of eggs was 24 laid and 9 dissected. These varied between 58 eggs laid with 2 dissected, and 24 laid with 25 dissected. In only very few cases was more than one of the dissected eggs fertile.

The length of time before the young larvae emerge from the eggs is dependent upon the time of the year and on the state of the weather. Those laid in the early spring are a few days longer in the egg than those laid in the late summer and early autumn. My records show that eggs laid in October emerged in 13 or 16 days, in November 11 or 12 days, in December 9 or 10 days, in February 12 or 14 days, and in March in 10 to 13 days. Two days before the young larva emerges, the egg becomes paler in colour and the black head of the larva is clearly seen through the egg shell. The young larva makes a break in the egg shell and gradually eats its way out and in most cases completely devours the empty egg shell.

c. *The Larva.* (Plate xxv.).

Mathew (14). Rainbow (19).

The young larva on emergence, no matter on what position of the foodplant the egg is laid, crawls to the young leaves at the centre of a shoot, and remains there for one or two days before feeding. In the first instar it usually feeds very early in the morning and remains hidden towards the base of a leaf during the rest of the day and night. When feeding it usually eats a subtriangular piece out of the young leaf. From the second instar onward the larvae usually feed in the early evening and hide head downwards in the shoots during the day,

though on a cold morning in May, 1923, I observed three young larvae feeding before 7 a.m. They cut a similar but larger subtriangular piece from the leaf when eating, rarely crawling towards the end of a leaf and eating right across. The larva in its first instar has a very large head for its size, being about twice the width of the widest part of the body, shining black with a very few long hairs; under a powerful lens it is seen to be minutely punctured; body pale green with paler longitudinal lines and about six long brown hairs to each segment; tail bifid, each division ending in a long whitish bristle. This instar lasts about 10 to 12 days.

The larvae in their remaining instars have an elongate rough pale green head with very short white hairs, longer towards the mouth which is black surmounted by white, eyes minute, black. The thorax and abdomen are usually pale yellow green, sometimes emerald green with several indistinct paler longitudinal lines, covered with minute white dots and very short white hairs.

The three thoracic segments are narrower than those of the abdomen, each segment has a number of transverse furrows, which are conspicuous when the larva is resting, but almost disappear when it is crawling. Tail bifid, with somewhat longer hairs and often tipped with pinkish. Spiracles minute, black. Ventral surface paler than dorsal. Legs pale cream. I have often found larvae of all the races with a broad reddish brown median dorsal band. Shortly before pupation the larva turns a pale bluish green. The duration of the larval period even for eggs that hatch at the same time is very variable and for eggs laid in the spring is from 3 to 5 months. For eggs laid in the autumn the larval duration is from 5 to 8 months. The figures show a full grown larva and one beginning to pupate (slightly enlarged).

d. *The Pupa.* (Plate xxv.).

Rainbow (19).

The pupa is bright yellow green or emerald green, and only rarely pale bluish green with the termina of wing cases outlined in bright yellow. It is short, stout, smooth with a slight projection on either side of the head. If the clumps of sword grass are thick it pupates, suspended by the tail from the underside of the larger drooping leaves, usually close to the ground, at other times it wanders away from the foodplant to pupate on neighbouring plants and in my cages it sometimes pupates on the sides of the cages. The pupal duration is dependent upon the time of the year that pupation takes place, as the following times show: August 41-45 days, September 29-39 days, October 24 days, November 19-26 days, December 18 days, January 18 days, February 17 days, April 28-34 days. The figures show a lateral and a dorsal view of the pupa (slightly enlarged).

When the pupa begins to show any colouration, the first parts noticed to darken are the ocelli of the forewing, then any of the paler markings and finally the ground colour. The following details apply to a pupa recently observed. On the evening of the 8th December, the ocelli could first be seen through the wing case; at 8 a.m. next morning the ocelli were very distinct and the pale markings could be seen and a median dark dorsal line appeared on the abdomen; by noon the whole of the wing had darkened, the ocelli being much darker; by 5 p.m. the thorax had darkened but not the whole of the abdomen; by 10 p.m. the whole abdomen was dark and drawn away from the pupal skin and the weight of the butterfly had caused an extension of the pupal skin between the fourth and fifth abdominal segments; at 6.30 a.m. the following morning a female emerged.

I had thought that the scales of the ocelli would show some marked differences from those of the other parts of the wing, but a microscopical examination has shown that this is not so. The scale illustrated (Text-fig. 2, No. 5) is from

a forewing ocellus, and the length and three anterior points are characteristic, both of the ground colour scales, and the orange scales. I found some few scales of the ocelli with four anterior points and a very few of the orange scales with only two anterior points. One butterfly watched emerge from a pupa gave the following details:—From the time of splitting of the pupa until the butterfly had completely crawled out, 40 seconds, and until the wings were fully expanded but still limp, 6 minutes; the hindwings expanded their full size before the forewings and the proboscis on emergence was pale grey, becoming dark brown later on.

e. *The Imago.*

They all have a weak irregular flight and confine themselves chiefly to the shade. The females are never found far from their foodplant, but the males like those of so many other butterflies are sometimes found playing round the hilltops. The females always emerge from their pupae early in the morning, usually about an hour before the males, and in a very few cases I have had males emerge in the afternoon. When the foodplant is growing in profusion, the males may be seen about 10 a.m. fluttering round clump after clump in search of the females, which are not so often seen on the wing. During sunshine the males are almost continuously on the wing, but when the sky becomes overcast they settle on their foodplant or some neighbouring shrub. During showery weather I have often collected large numbers by picking them from their resting places with forceps. If cliff faces or overhanging ledges are near the foodplant, they very often spend the night in these positions.

They first appear on the wing from Sydney north in the month of August and continue until May, but predominate during September and October, and again in March and April. In more southern latitudes they are not on the wing until late in September, and in the higher parts of the Main Divide not until late in October. I have not been able to determine the length of time the butterflies themselves live in nature, but it is probably as long as a month. A male lived for 4 days without feeding and a female for 7 days in the open without feeding, whilst with artificial feeding I have kept specimens as long as 15 days.

Pairing usually takes place during the morning, and in all the cases I have observed has never lasted longer than 23 minutes. This short length of time no doubt accounts for the fact that this species is seen so rarely in copulation in the bush. One male has been known to pair with more than one female, and on at least two occasions the female has been paired with the male twice. I am strongly of opinion that in nature after about half of the eggs are laid a further copulation is necessary before the remaining eggs are laid. I have never observed that any eggs are laid before the female has paired.

The records of the time from the laying of the eggs until the butterfly emerges shows that eggs laid in October produce butterflies in 3½ to 6½ months, in November in 3½ to 6 months, in December in 3 to 4 months, in March in 7½ to 8 months, and in April 7 to 10 months. Taking separate families, I found that eggs laid by the same female from 31st October to 7th November produced butterflies from 25th February to the 13th May, and eggs laid by another female on 18th and 19th April produced butterflies from 13th November until 13th February. In every family with very few exceptions the males were the first to emerge, then males and females, and towards the end of the period only females. In some cases the percentage of butterflies reared from eggs was very high, reaching up to 80 per cent. The percentages from eggs laid in the spring was always much greater than for eggs laid in the autumn owing to the larvae being subjected to more rigorous conditions during the winter.

The antennae are less than half the length of the costa of the forewing, with clubs long, gradual and very slender. Eyes smooth.

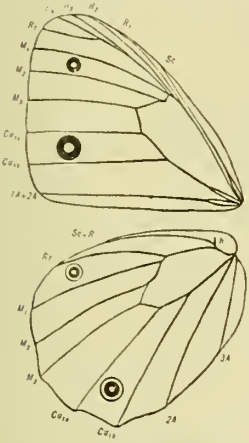

Fig. 1.

The forewing venation shows the basal portion of the Subcostal (Sc), Cubitus (Cu) and Anal (1A. + 2A.) veins swollen: R_2 arising close to the end of the cell: M_1 longer than M_2. In the hindwing the media has three and the cubitus two branches, and the humeral veinlet (h) is short and not well developed.

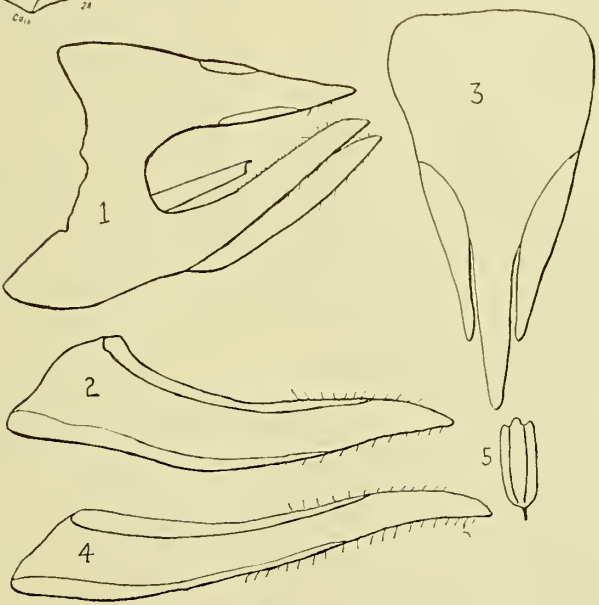

Fig. 2.

The male genitalia do not depart in any marked degree from the ordinary Satyrid type. Text-figure 2 gives a much enlarged profile view of the genitalia of *abeona* (1); a view from below of the uncus still further enlarged (3); whilst much enlarged views from the inside of a valve of *abeona* (2) and *morrisi* (4) are given. An examination of several specimens of both these races shows that there is no appreciable differences in their genitalia.

In the coastal districts of New South Wales the butterflies are extremely common in the spring and again in the autumn, as many as a dozen or more being seen at one time. In some districts many thousands of plants of *Gahnia* are to be found growing in the one swamp. In the mountains they are not so plentiful, but when the foodplant is located near a stream they can readily be found.

TISIPHONE ABEONA ALBIFASCIA Waterhouse.

Proc. Linn. Soc. N.S. Wales, 1904, p. 468. Waterhouse (25), Plate I., figs. 23, 27, 28. Waterhouse and Lyell (29), fig. 816. *Epinephile abeona* Anderson and Spry (1), figured.

This is the Victorian race which extends into the southern coastal districts of New South Wales. Above in the forewing, the postcellular pale bar is much broader than in *abeona* and is cream in the female; the broad central area is slightly paler than in *abeona* and sometimes in the male and usually in the female is cream where it crosses the cell; the ocelli are usually larger than those of *abeona*, and the white pupils are larger than in *abeona* and the blue scales surrounding them more extensive. In the hindwing the ring to the subtornal ocellus is always more conspicuous than that of *abeona*, and there are sometimes, especially in the females, indications of an inner subterminal pale band.

Beneath the white markings are always much more conspicuous than those of *abeona*, especially the discal and two subterminal white bands of the hindwing. Fig. 816 *albifascia* and Fig. 815 *abeona* in the Butterflies of Australia (29) show the distinctions of the undersides very well.

Holotype male Wandin December 10, 1899; Allotype female and Paratype male and female Wandin without date are in my collection.

In addition to the dates already given (29), I have it from Wandin (which includes Fern Tree Gully), in September, and Mr. J. A. Kershaw records its occurrence at Wilson's Promontory from early November to February.

Mr. C. H. Borch gives me the following Victorian localities:—Wilson's Promontory right to the southernmost point in December; Upper Beaconsfield in May and December; Bayswater in January; Belgrave in November and December.

The change to the typical race *abeona* appears to begin about Narooma, six specimens I collected there showing a slight diminution of the size of the white bands on the hindwing beneath. Specimens from Kiola about 60 miles further north are almost typical *abeona*.

I have had numerous larvae sent me in the spring from Macedon and Fern Tree Gully, and the butterflies emerged in Sydney from September 30 to December 31. The pupal duration of those emerging early in December was 19 and 20 days. Larvae from Eden produced butterflies in Sydney from December 15 to February 6. Larvae I found at Narooma in October gave me the following results: Larva pupated November 2, male emerged November 28, larva pupated November 5, female emerged November 29, the butterfly was also caught at this place in October.

This species varies somewhat in size, some females being very large, the markings beneath also vary in size, but are always much more conspicuous than those of *abeona*. One interesting male I have from Fern Tree Gully (emerged Sydney, October 10) has on the hindwing above, an obscure reddish brown discal band, a female also from the same place (emerged February 23) has a similar band, but broader and paler, whilst another male caught at Fern Tree Gully (November 21) is like the first male. The presence of this band on the hindwing above shows that the influence of the northern race *morrisi* is not wholly lost in Victoria.

TISIPHONE ABEONA ABEONA Donovan.

Donovan (7), pl. xxii., fig. 1; Godart (9); Boisduval (2); Standinger (22), pl. 81; Rainbow (19); Fruhstorfer (8); Waterhouse (25), pl. i., figs. 21, 22; Waterhouse (28), pl. ii., fig. 1; Waterhouse and Lyell (29), figs. 75, 76, 815.

Donovan's figure (7) represents the upper and underside of a female, it is somewhat more highly coloured than specimens found near Sydney at the present day. An examination of all Donovan's figures shows that they are all more or less inaccurate and usually too bright. As the specimen is said to come from Port Jackson and considering the early date (1805) it could not have come from anywhere else, and also as the figures agree much better with Sydney specimens than they do from anywhere else, Sydney must be taken as the type locality.

Hübner (10), unaware of Donovan's figure, gave coloured figures of the upper and underside of a male under the name *zelinde*. These figures are good, much better than those in the reissue (13) and undoubtedly represent the Sydney race. Godart (9) describes both male and female, but makes no mention of *zelinde*, but all subsequent authors mention *zelinde* as a synonym of *abeona*. The figures given by Standinger (22) and Fruhstorfer (8) are both males and undoubtedly this race.

This race is distinguished from *albifascia* by the dull red surround to the subtornal ocellus of the hindwing above (in this it also differs from *aurelia*), and by having the white bands beneath very much narrower, often reduced to a white line. Only rarely do the orange bands of the forewing above show any cream towards the costa and beneath these same bands show much less cream.

This race occurs along the coast from Kiola to the southern bank of the Hunter River wherever the foodplant is growing, and is practically continuous over this area, being absent only where advancing civilisation has destroyed its foodplant. It also occurs in any of the gullies between the coast and the Blue Mountains, but is absent from the plains between Parramatta and Penrith. It occurs in suitable places in the Blue Mountains up to 4,000 feet. Dr. E. C. Chisholm records it from Marrangaroo, I have taken it further north near Ilford and Dr. N. W. Hansard tells me it occurs near Rylstone. At Sydney, within a mile of the sea, it is found from August to April, but on the mountains, it appears later and ends earlier.

Three very interesting aberrations of this race are in my collection. A female from Woodford, 2,000 feet, in October, which has the subtornal ocellus of the forewing over twice the usual size; a male from Stanwell Park, 1,000 feet, in October, which has no orange postcellular bar on the forewing above and beneath. On the hindwing beneath there is no discal band, the outer subterminal band is absent, but the inner one is present, broader and obscure; the third specimen is a male, Wentworth Falls, 2,800 feet, in January, caught by Mr. G. M. Goldfinch, in this specimen there is a complete absence of orange above, the bands being white, and the surround to the subtornal ocellus is brown and not dull red. On the underside the postcellular bar of forewing is white, the broad band is white in the cell and yellow below the cell, on the hindwing the surround to the ocelli is brown. When Mr. Goldfinch saw this specimen first he mistook it for the female of *Het. mirifica*, until he noticed the difference in flight.

TISIPHONE ABEONA AURELIA Waterhouse (26).

Australian Zoologist, p. 50, 1915; Waterhouse (25), fig. 26 (as *joanna*).

This is another of the orange handed races and can be distinguished from the typical race by its brighter orange markings and the more prominent markings beneath. Its chief difference from *abeona* is that, whilst it has the general appearance of the southern races, it has orange rings to the ocelli of the hindwing.

The type series of this race were caught by me at Nelson's Bay, Port Stephens. I have had about 30 specimens from this locality and they do not show any marked variations, except that in some females there is a trace of the pale discal band on the hindwing above. My two Tuncurry specimens are similar. From Coopernook, Manning River, I have had about 50 specimens, most of which agree with those from Port Stephens, the discal band on the hindwing above is more often present and is orange. In some few males the broad orange band of the forewing is reduced where it crosses the cell. In some females the postcellular bar of the forewing above is cream and not orange. Two interesting specimens have the broad orange band of the forewing above almost divided by a vertical irregular brown band. None of the specimens is cream above.

From near Camden Haven and a few miles further south, I have examined over 100 specimens, which show the same variations as those from Coopernook, some males have the orange band of the forewing above reduced in the cell to an ill-defined patch not connected with the well-defined portion below the cell. The females show an orange discal band on the hindwing above in many cases. From this locality I have a male and two females which have cream bands on the wings above and are very close to figure 795 of *joanna,* Waterhouse and Lyell (29).

Coopernook is about 70 miles distant in a direct line from Nelson's Bay, Port Stephens, whilst the locality near Camden Haven is about 15 miles further north. Port Macquarie is a further 20 miles north.

The above localities to which I restrict the race *aurelia* show at Nelson's Bay typical *aurelia,* at Coopernook the influence of the northern race begins, that is after crossing the Manning River and it is more evident near Camden Haven.

Described from a series of specimens in my collection caught in October, 1914, at Nelson's Bay, Port Stephens, or reared from larvae taken at the same time. Holotype male emerged in Sydney, November 27; Allotype female emerged November 27; Paratype males (9), October 25 to December 7; Paratype females (5), October 25 to November 14. The pupal duration is about 15 days at this time of the year.

Localities: Port Stephens, March, October to December; Tuncurry, April, May; Coopernook, April, October, November; Camden Haven, April, October. Very probably occurs at all these localities from August to May.

Tisiphone abeona joanna Butler.

Enodia joanna Butler (3); Butler (4), pl. iv., fig. 8; Waterhouse (25), pl. i., figs. 1-14, 16-18, 29, 30; Waterhouse (28), pl. ii., figs. 2, 4-15; Waterhouse and Lyell (29), figs. 102, 794-814, 816; not *T. joanna* Waterhouse (23).

I have now seen over 400 specimens caught chiefly by myself within eight miles of the post office at Port Macquarie. Amongst this large number of specimens there is no particular form that predominates. We find specimens on the one hand that if they had been caught 50 miles further south would be considered typical *aurelia,* others if caught 50 miles further north would be considered typical *morrisi.* Between these two extremes every intergrade is found, specimens with the colour of *morrisi* and the shape of markings of *aurelia* and vice versa. In some few cases the markings are reduced and approach *rawnsleyi* very closely. I have given many illustrations (some in colours) of these variations as shown in the references above and also in the Butterflies of Australia (29); fig. 102 is taken from an illustration of the type in the British Museum.

I have already suggested that the type reached England early last century, very probably through the instrumentality of Alexander Macleay. Until I had

received the coloured drawing of the type in the British Museum I had considered the race *morrisi* to be *joanna*.

I have specimens of this race from Port Macquarie, from September to May (except December), no doubt it is also caught there in August and December. Dr. E. C. Chisholm has sent me two males from the Comboyne, March and April which belong here.

TISIPHONE ABEONA MORRISI Waterhouse.

Plate xxvi., figs. III., III. A., IV., IV. A.

Waterhouse (25), pl. i., figs. 19, 24, 25; Waterhouse (28), pl. ii., fig. 3; Waterhouse and Lyell (29), figs. 77, 78, 817.

This is the coastal race, extending from the Macleay River to Southport, in Queensland, and I also include here my specimens from Crescent Head, about 20 miles north of Port Macquarie, in September, as nearly all of the 20 specimens agree with *morrisi*; the most notable example is a female, which has a yellow tinge in the broad band on the forewing above; this band also extends somewhat into the cell; two other specimens show a trace of this extension into the cell. These specimens occupy, at the end of the southern range of *morrisi*, a similar place that the specimens from near Camden Haven occupy at the end of the northern range of *aurelia*.

The figures on the plate accompanying this paper show this race very well, and also show how different it is to the race *abeona*. The fact that I have been able to pair *abeona* and *morrisi* is sufficient to show that they are geographical races, even without the further evidence of the intermediate hybrid race *joanna*.

The type series were all caught at Ballina, Richmond River, chiefly in September and October, 1902. They consist of the following in my collection: Holotype male, September 29, 1902 (fig. 24 in 25); Allotype female, February 5, 1898 (fig. 19 in 25); eight Paratype males, January 1, 1898, and the others October, 1902 (one of which is fig. 77 in 29), and seven Paratype females, all October, 1902 (one of which is fig. 817 in 29).

Localities: Richmond River (type locality), September to April; Southport, Queensland, December; Tweed Heads; Clarence Heads to the Macleay River, September, October (numerous specimens collected over the whole coastal area); in addition Urunga, Bellinger Heads, November to March.

In my catalogue (23) I used the name *joanna* for the specimens of this race I had taken prior to that date and distributed many of these specimens under that name.

On the road from Coff's Harbour to Dorrigo I have a fine series of specimens. Those at Coff's Harbour are ordinary *morrisi*, and so are those from Ulong (November), about 20 miles away, and at an elevation of about 1,500 feet. From Dorrigo, I have two series of specimens,—one lot caught by Dr. R. J. Tillyard, in December, 1911, and the other by Mr. W. Heron, in November, 1914. These specimens are from an elevation of over 3,000 feet, and are larger and finer, with more white markings than coastal specimens. I regard these as the next race *regalis*, but not quite typical. Mr. Heron's specimens are labelled E. Dorrigo, within 15 miles of Dorrigo, and Dr. Tillyard's Dorrigo, which is about 20 miles from Ulong.

The upperside male on Plate xxvi. is from Urunga and the underside male from Macksville, both figures slightly larger than natural size. The figures of the females are from paratypes taken at Ballina, in October, 1902.

TISIPHONE ABEONA REGALIS *subsp. nov.*

Plate xxvi., Figs. I., I. A., II., II. A.

Male. Above. Forewing dull black: a postcellular bar and a large subtornal patch, white: a small subapical ocellus and a large subtornal ocellus, deep black, the former faintly ringed white and both white-centred and sprinkled with blue scales: cilia blackish. Hindwing dull black: a broad irregular discal band, white: a small subapical deep black ocellus, centred white and surrounded with a yellow-brown ring, a similar larger subtornal ocellus, centred white, sprinkled with blue scales and surrounded orange-red: usually a small white spot below the subapical ocellus and another above the subtornal ocellus. Cilia white, at veins black.

Beneath. Forewing dark brown: markings as above, but more extended, subtornal patch extended as a broad white bar across cell and as well nearly joining the subapical bar: ocelli distinctly ringed cream: two subterminal white lines, inner more distinct: usually two white spots between the ocelli: cilia black and white. Hindwing dark brown: markings as above, two subterminal white lines, inner more distinct: both ocelli ringed orange-red. Cilia white, at veins black.

Female. Above as in male: white markings much broader and a faint white spot near end of cell in forewing and traces of an inner white subterminal line on both wings and an outer white subterminal line on hindwing: subapical ocellus of hindwing ringed dull orange-red.

Beneath as in male; white markings broader and more distinct and an additional irregular white surround to the four ocelli.

There is not much variation in the males, which are not in the best condition. In the females the chief variation is in the size of the cell patch in the forewing above; in one specimen this is as distinct as it is beneath.

It differs from the race *morrisi* by the slightly darker colour above, the much broader white markings above and beneath, especially the very extensive subtornal patch and the cell bar of forewing beneath.

Holotype male (fig. I.), February, 1925; Paratype male (fig. I.A.), January 26, 1922; Allotype female (fig. II.A.), January 26, 1922; Paratype female (fig. II.), emerged from pupa in Sydney, October 25, 1922. Also 12 paratype males and 12 paratype females December 16 to February 5, all from Barrington Tops, New South Wales.

I found this race sparingly when I visited Barrington Tops in January, 1922, and again in January and February, 1925. On both occasions eggs and larvae were found, and some of these produced butterflies at Sydney in October. The name is given as the type locality is at the end of the Mount Royal Range. The specimens caught by Dr. R. J. Tillyard at the Dorrigo in December, 1911, and by Mr. W. Heron at East Dorrigo in November, 1914, belong to this race, as does a specimen from near Hanging Rock on the Main Divide. Types in my collection.

This is a large and magnificent race, larger than any of the others. It appears to be confined to an altitude of 3,000 feet and over, and will probably be found in many other places on the Main Divide of this altitude. The type locality is due west of Tuncurry, where an orange race occurs and for at least 40 miles further north the same orange race occurs, so we have over a distance of at least 40 miles, a broad handed orange race (*aurelia*) on the coast and over the same latitude on the Main Divide a narrow white handed race (*regalis*).

TISIPHONE ABEONA RAWNSLEYI Miskin.

Epinephile rawnsleyi Miskin (15); Waterhouse (25), pl. i., figs. 15, 20; Waterhouse and Lyell (29), figs. 82, 83.

This race is smaller than those found in the south and is a very sombre insect. Above it is brown black, with the ocelli of the forewing deep black, rarely in the male, usually in the female, ringed with pale yellowish, those of the hindwing deep black, conspicuously ringed with orange red. On the underside the white markings are much reduced in size.

In many specimens, especially in the female, there are traces of a white discal band on the hindwing above; this more often appears basad of the ocelli and in none of my specimens forms a complete band as in *morrisi*. Two females show a white streak basad of the subtornal ocellus on the forewing above.

This race is well described as a small form of *morrisi* that has lost or nearly lost all the white markings above.

The type series is in the Queensland Museum from the Maroochy River, Queensland, later Miskin (16) gives the locality as Mooloolah, where the race is very common. I have it from Caloundra, October; Mooloolah, October to December; Palmwoods, October, March, April; Nambour, October; Eumundi, March.

TISIPHONE HELENA Olliff.

Epinephile helena Olliff (17); Olliff (18), figured; Fruhstorfer (8), pl. 94; Waterhouse and Lyell (29), figs. 84, 85.

The type of this species is from Mount Bellenden-Ker (about 3,000 feet) and is in the Australian Museum, Sydney. Otherwise I only know it from near Kuranda (about 1,000 feet) and Mr. A. N. Burns has taken it near Gordon Vale at about 500 feet. The swamps near Cardwell should be searched to see if it occurs there. The species has an appearance quite unlike that of *T. abeona* and reminds one of the much larger *Morphopsis* from New Guinea.

Mr. C. H. Borch has a record of this species at Highleigh (about 1,300 feet) in the Gray Ranges, south of Cairns, in November.

Its Distribution.

In September and October, 1914, I made a rapid survey of the coast line between Coff's Harbour and Ulladulla, collecting at over twelve distinct localities and extended my collecting to the Blue Mountains at about 2,000 feet. Mr. H. W. Simmonds collected *rawnsleyi* from Mooloolah in October of the same year, and in November collected at Bermagui, Tathra and near Eden. Mr. W. Heron, in October, collected at six different localities between Yamba and Coff's Harbour, and in November sent me specimens from Ulong and East Dorrigo. Mr. S. J. Turner sent me a long series collected in October from Kiola, south of Ulladulla. So in this spring of 1914, the only gap in the collecting approaching 50 miles in the stretch of coast from Yamba, Clarence Heads to Eden, was the gap between Kiola and Bermagui, which I have since partially filled by collecting at Narooma. In November and December of the same year, I also received specimens from Macedon, Fern Tree Gully and Wilson's Promontory, in Victoria. This one set of collections amounted in all to nearly 600 specimens. Before 1914, I had made three collections at the Richmond River, and also at many intermediate localities in the range of the race *abeona*, both on the coast and in the mountains. Since 1914, I have collected several times at Urunga, Port Macquarie, Camden Haven, Coopernook, and have received many specimens of *rawnsleyi* from South Queensland and *albifascia* from Victoria. Besides this I

Fig. 3.

This shows the coastal distribution of six races of *Tisiphone abeona*, and at A. the localities of the race *regalis*. C. is the approximate position of the Comboyne.

have had two trips to the Barrington Tops and collected the new race *regalis* there. In all I must have examined over 2,000 specimens of the various races of *abeona* in my own and other collections.

For *T. helena* I have had to rely on my friends, Messrs. R. E. Turner and F. P. Dodd, as I have been to Kuranda only during June and July, when this species is not on the wing.

Text-figure 3 shows an outline sketch of the coast line of New South Wales, together with portions of South Queensland and South-east Victoria. The sketch is modified from that previously published by me (27). An examination of this map, together with that of the localities, shows that I have an almost continuous range of specimens from Southport to Eden, a gap occurs in the north between Southport and Caloundra, and in the south between Eden and Wilson's Promontory. With regard to the first, I have very little information, but I doubt if the foodplant now exists between Caloundra and the Brisbane River. On the south, the species no doubt occurs in many localities between Eden and Wilson's Promontory.

At an elevation, the collecting has not been so extensive nor continuous. The southern race has been taken at Mount Macedon and in the Dandenongs. It is doubtful if it occurs in the Victorian Alps, where several experienced collectors have collected. At Mount Kosciusko, it must certainly be absent, for this spot has been more intensively collected than any place in eastern Australia, above 3,000 feet. It appears in suitable places in the Blue Mountains and the portions of the Main Divide nearby. I searched for it very carefully on the low portion of the Main Divide, known as the Cassilis Gap and again on the Divide near Murrurundi, but without success. It appears again at Barrington Tops, on a spur from the Main Divide, at Hanging Rock, on the Main Divide, and again, near Dorrigo, on another spur from the Main Divide. Further collecting is necessary to determine how far the various races are distributed along the Main Divide.

The seven races fall naturally into two pairs of three with the intermediate hybrid race at Port Macquarie. The three races from the south have a very broad orange band on the forewing above and no pale band on the hindwing above. These three races differ from one another only in degree. The Victorian race *albifascia* occurs, both at the coast and in the mountains to about 2,500 feet, and on the coast from north of Bermagui passes almost imperceptibly into *abeona* at Kiola, there being no barrier to keep the two races entirely distinct, though the extremes at the type localities are abundantly distinct.

The Sydney race *abeona* is at times very common and is also found both on the coast and in the mountains, the most southerly mountain record being near Bowral and the most northerly near Rylstone. At the present day, there is a definite barrier between *abeona* and the next race *aurelia*. This is the large swampy area of the estuary of the Hunter River and also the extensive settlement surrounding the city of Newcastle. North of the Hunter River, there is also the long stretch of sanddune country behind the Stockton Beach which does not now, if it ever did, have the foodplant growing. There is at the present time no chance of the races *abeona* and *aurelia* ever mixing.

The swampy areas at the Hunter River are of a different type to those in which the foodplant grows so readily at other places on the coast, and they probably never at any time had *Gahnia* growing in them.

The area occupied by the race *aurelia* is not very extensive, from Port Stephens to Camden Haven, and it is only in the southern parts of this range that it is constant; to the north, there is an occasional mingling with the next

race *joanna*. The race *aurelia* does not occur in the mountains to the west, where it is replaced by one of the northern races *regalis*.

The race *joanna* occupies a very limited area around Port Macquarie, where it is very common and very variable. I visited the Comboyne in 1914, but failed to find *Tisiphone*, but Dr. E. C. Chisholm has sent me two males from there. He says it is very local and far from common. A fuller discussion on the race *joanna* appears in a later portion of this paper.

The three northern races also differ from one another in degree and may be described as having narrow white bands on the forewing above, and a white discal band on the hindwing above.

The race *morrisi* occupies a long stretch of coast north of Port Macquarie into southern Queensland. North of the Macleay River, it is very constant, but at Crescent Head, some 20 miles north of Port Macquarie, it shows some influence of the southern races, due to an occasional mingling of a specimen of *joanna*. The water of the creek near Crescent Head flows south to join the Hastings River which enters the sea at Port Macquarie. At Southport the race *morrisi* seems to have disappeared. Mr. R. Illidge caught it there many years ago, and in July, 1919, accompanied me there, but, though I spent many hours searching the foodplant, which was very plentiful, I could find no trace of larvae. Larvae of *rawnsleyi* were obtained by me at Mooloolah, only a few days before our visit to Southport.

The race *regalis* only occurs in the mountains and its range owing to insufficient collecting chiefly, cannot be accurately delimited. The southern range is certainly Barrington Tops, but the northern is doubtful. The race is the finest and most heavily marked of them all.

The race *rawnsleyi* is a small and dark one, with the white markings above almost absent. It is confined to a small area between Brisbane and Gympie. With the exception of Caloundra on the sea coast, all the records are from near stations on the railway line from Landshorough to Eumundi inclusive. Now, as probably in the past, the estuary of the Brishane River forms the barrier between this race and *morrisi*. I found larvae in quantity at Mooloolah in July, 1919, and since then I have had many specimens from there. This race requires much more investigation. The question should be settled as to whether Caloundra is its southern limit and how far north does the race actually extend.

From this race north to the Cairns district no *Tisiphone* have been found. Extensive collecting has been done near Rockhampton, Mackay and Townsville. In 1923, I visited Eungella in the Ranges, 45 miles west of Mackay and, though *Gahnia* was found, no larvae of *Tisiphone* could be discovered after a very careful search.

In the Cairns district *T. helena* occurs and always at some elevation above sea level.

Although the foodplant is found in Tasmania, especially on Mount Wellington, *Tisiphone* has not been recorded from there. Such a conspicuous species could not possibly have been overlooked.

Position of Tisiphone amongst the other Australian Satyrids.

Of all the groups of butterflies in Australia, the Satyrids exhibit in a marked degree the two distinct elements in the Australian fauna. These consist of a comparatively recent migration from the north, entering Australia by way of a late Pliocene or early Pleistocene connection with New Guinea across the present Torres Straits. These Satyrids are typical of the Torresian Region and have advanced southwards along the east coast of Australia to meet the older Satyrids, which now have their central location in south-eastern Australia. One or two

species have extended westward along the north coast and have reached at least as far as Port Darwin. The migrants from New Guinea all belong to well known genera, and probably entered Australia at two or perhaps three different periods of time. The genus *Hypocysta* was the first to arrive and has extended along the east coast nearly to the Victorian border. This genus has a limited range in the Indo-Australian Region, besides Australia it is only found in New Guinea and some of the neighbouring islands. Of the six Australian species five are endemic, the remaining form has only advanced a short distance down the Cape York Peninsula. The endemic species have a facies considerably different from the New Guinea species. They have been accompanied on their travels by the single species of *Yphthima*. With *Yphthima*, the remaining genera *Melanitis*, *Mycalesis*, and *Orsotrioena* have a very extended range, reaching as far westward as India and Ceylon. It is very noteworthy that the two wideranging species of *Mycalesis* and *Orsotrioena* have not extended so far south as the two purely Papuan species of *Mycalesis;* this is another argument in favour of two separate and distinct migrations from the north into Australia.

All the species of the above genera have two distinct broods in the year; exhibit in many cases strong seasonal dimorphism; with the exception of *Hypocysta adiante* have not developed any marked geographical races in Australia and with the one exception of *Yphthima arctuous*, the heads of the larvae are distinctly horned. These Torresian species found on their arrival the south-eastern portion of Australia (the Bassian Region) in possession of a very distinct endemic group of Satyrids; species belonging to the genera *Heteronympha*, *Argynnina*, *Oreixenica* and *Xenica*, that have only a single brood during the year; that have in most cases developed in one or other of their stages marked specialisation and have amongst the widespread species developed marked geographical races, so marked as to be considered distinct species by some entomologists. The only species that could be questioned as having two broods during the year is *Argynnina cyrila*, normally appearing on the wing in the early spring, and a few specimens of which have been reported to have been taken in the autumn. I have recently proved that the normal pupal duration of this species near Sydney is seven months (February to August) and that the pupal envelope is particularly thick to withstand the winter, but it is quite possible that under special climatic conditions a few specimens might possibly emerge during the autumn. Though I have often searched its haunts during the autumn, I have never been able to see one on the wing myself. These Bassian species have in some cases their early stages specialised. *Heteronympha merope*, *H. philerope*, *H. paradelpha*, *Oreixenica orichora* and *O. latialis* have their larvae without prominent horns to their heads, their pupae are smooth and lie unattached on the ground. The larvae of *H. mirifica*, *H. banksi*, *H. solandri*, *Argynnina hobartia*, and *Xenica acantha* have prominent horns on their heads, and the pupae hang suspended by the tail, as do the pupae of *O. lathoniella*, *O. correae* and *X. klugi*. (I do not know the life-history of *Heteronympha cordace*). All the species of these four genera have one brood in the year. Fruhstorfer's suggestion that *ella* (8, p. 304) and *suffusa* (8, 305) are dry-season forms of *X. kershawi* and *H. merope* is therefore not tenable. The first is a northern race of *O. kershawi* and the second a *melanic aberration* of *H. merope*. Seasonal dimorphism is found only rarely in Australia, and is quite absent in the south. Geographical variation and sexual dimorphism on the other hand are frequently met with.

As an illustration of the life-history of a Satyrid of south-eastern Australia, I have figured (pl. xxv.) that of *Oreixenica latialis*. This species as far as is known is confined to Mount Kosciusko above 5,000 feet. It was described and figured (29, p. 43, figs. 823, 824) as an alpine subspecies of *O. lathoniella*. Suh-

sequent to the publication of the description in 1914, I found the early stages of both and they differed, so in 1923 (28, p. xviii.), I raised *O. latialis* to specific rank. Though the larvae are very similar in both these species, the pupae are very distinct. The pupa of *O. lathoniella herceus* is attached by the tail and hangs suspended head downwards: its dorsal surface has a number of transverse ridges. The pupae of *O. correae* and *O. kershawi* are somewhat similar. On the other hand the pupa of *O. latialis* is smooth, and it lies unattached on the ground or amongst tufts of snow grass on which the larvae feed. I found at Mount Kosciusko that along Digger's Creek the ranges of *O. latialis* and *O. lathoniella herceus* overlapped for a distance of about two miles in length and about 400 feet in elevation, the former being caught from above the waterfall up to Pretty Point, whilst the latter from the hotel to the junction of Digger's Creek with the Snowy River. In February I only caught one specimen, but it was very common in March of the same year.

Larvae found at Kosciusko in December and brought to Sydney where they pupated emerged at the end of February with a pupal duration of 16 days. Eggs laid at Kosciusko in March and brought to Sydney gave me butterflies the following summer from December 26 to January 21, with a pupal duration of 21 to 22 days. Pupae left lying on a smooth, flat surface produced perfect butterflies.

The genus *Tisiphone* does not fall completely into either of the above groups. Its range is greater than and inclusive of the range of such Bassian species as *Heteronympha mirifica, H. banksi, H. paradelpha, Oreixenica kershawi*, and *O. correae*, though it has not reached as high an altitude as *O. correae*. These, however, belong to a later development in the Bassian fauna, as they also have not reached Tasmania. *Tisiphone* also occurs much further north than any Bassian Satyrid. It shows no seasonal variation, but has developed in a marked degree geographical races. It is single brooded at a high elevation, where the period of warm weather is not sufficiently long to complete two broods in twelve months. Though in many cases on the coast two broods are produced in one year, the duration of the larval stage from the same batch of eggs is so variable, that only a proportion of the eggs laid in the autumn produce in the following spring butterflies that in turn give rise to butterflies the next autumn. The year 1923 showed in a marked degree the effect of weather conditions on this species. Many eggs that were laid in the autumn gave butterflies up to December, whilst some larvae from the same family were only half grown in January, 1924, and did not produce butterflies until the autumn. For the season September, 1923, to March, 1924, the species must then have been both single and double brooded in the same family.

In its relation to the Torresian fauna *Tisiphone* has extended much further south than any of the Torresian Satyrids. I am of opinion that *Tisiphone* belongs to a very early migration from New Guinea, a migration small in number of species (including *Papilio macleayanus*) and that eventually in the mountains of New Guinea a near ally of *Tisiphone* will be found as has already been done in the case of *Papilio macleayanus* and still more recently a form of the wide ranging but discontinuously distributed *Argynnis hyperbius* has been discovered at over 4,000 feet in New Guinea.

Since *Tisiphone* has developed well marked geographical races and has a range extending beyond any Torresian Satyrid, its appearance in Australia must have been earlier than these. Since it has not reached Tasmania, where its food plant is found, its appearance must have been after the Bassian Satyrids that occur there.

The Problem of the Race joanna.

One problem of importance has been clearly indicated in what has been written above and that is the explanation of the great variation shown amongst the numerous specimens of *Tisiphone* caught in the Port Macquarie district. This variation is so great that, if say, a dozen specimens were selected and submitted to many a competent entomologist unacquainted with their history, they would without hesitation all be considered distinct species. The problem then was to account for this variation as from the field observations they could only be a single variable race. I then proposed that *morrisi* and *rawnsleyi* were not distinct species as had been thought, but only geographical races of *abeona* and that *joanna* was a race made up by the crossing of the broad orange banded southern form with the narrow white banded northern form.

The Proof that the Race joanna is a Hybrid Race.

This proof has been established in two different ways, but the apparatus used and method adopted require explanation. It is essential to have the growing foodplant under continual observation. I therefore brought home many plants of sword grass and placed them in wire gauze cages about 3 feet high and 2 to 3 feet wide and deep. These cages were so constructed that larvae could not escape and that parasites, unless extremely minute, could not enter. They were all marked with a letter or number for reference. In order to obtain the maximum efficiency from the cages, which were limited in number owing to their cost, pairings were not made in the cages themselves. A number of sword grass plants were grown in kerosene tins and several special wire cylinders made three feet high and two feet in diameter. One of these cylinders was placed over the foodplant growing in a tin and the top of the cylinder covered with mosquito net. The butterflies readily paired in these cages and, according as few or many eggs had been laid, the tin of sword grass was removed to the numbered cages containing the best amount of growing sword grass to feed the larvae. As soon as it was ascertained that pairing had taken place the male was killed and set and the female kept alive by feeding as long as possible. The method of feeding was to use about four tablespoonfuls of sugar dissolved in an ordinary cup of water. The butterfly was held in a clip made by slitting down a small piece of bamboo which gave sufficient spring to hold the butterfly. In most cases as soon as the butterfly was placed over the sweetened water, it uncoiled its proboscis and extended it to the liquid. If the butterfly did not attempt to feed, the proboscis was uncoiled by using a pin, and always when the butterfly was placed over the sweetened water the second time, it uncoiled its prohoscis itself. The cages proved very satisfactory, and the only enemies that could not be entirely eliminated were spiders, which when very young could enter through the wire mesh, but a daily search reduced this pest almost to a negligible quantity. The cages were of a size easy to search, and when the larvae pupated they were removed from the cages and labelled, and so were under more direct observation until the butterflies emerged. Two distinct methods of proof of the hybrid nature of the race *joanna* are described below (a) by rearing to butterflies from females caught at Port Macquarie, (b) by pairing specimens of the races *abeona* and *morrisi*.

a. *By Breeding from Females of the Race joanna.*

On April 17, 1922, I caught two females of this race at Port Macquarie and brought them alive to Sydney. I caged them separately with growing plants of sword grass. Specimen E. laid altogether 14 eggs and was killed on April 19. Specimen D. laid 9 eggs and during my absence escaped and could not be found. Specimen E. produced 12 butterflies, six males and six females. These, with their

mother, have already been described and figured (see Waterhouse (28), pl. ii.). They show that of the twelve specimens nine had orange and three had white markings, and that the markings were not identical. This family showed the sexes in equal numbers, but four males emerged before the first female, followed by two more males and then four females; though the eggs were all laid within two days of one another and hatched within two days of one another, the difference in time of appearance of the first and last specimens was three months, whilst the difference in time between the first and last male was a little over one month: the difference in time between the first and last female was about two months and a half.

The mother of this family was marked above somewhat like *morrisi* with the colour more like *aurelia*, but the shape of markings of the offspring was much more like *aurelia* than *morrisi*, and the colour of nine of the twelve specimens was that of *aurelia*.

The other family consisting of two males and three females was the offspring of a pale coloured female, and the specimens obtained showed a greater likeness to *morrisi* than *aurelia*, one female was almost a typical *morrisi* and the males close to it. The other females were close to *aurelia*, but both showed traces of a pale band on the hindwing above.

The great differences shown in both colour and shape of markings of the seventeen specimens of these families prove that *joanna* is by no means a pure race, but made up from the broad orange banded southern form mating with the narrow white banded northern form.

b. *By Pairing the Races abeona and morrisi.*

In the late winter and spring of 1920, the initial steps were taken to begin this experiment. A large number of larvae of *abeona* were collected near Sydney, about 400 in all being obtained. These when they had pupated were kept carefully under observation. Early in October a trip was made to Urunga at the mouth of the Bellinger River, where about 100 larvae of *morrisi* were obtained; these were brought to Sydney and allowed to pupate. Urunga was chosen as a suitable spot as the foodplant was plentiful, and it was sufficiently far north to be beyond any possible influence of the orange banded races south of Port Macquarie. When suitable butterflies emerged and the weather conditions were satisfactory, I made my pairings and secured ten sets of fertile eggs, having five pairings with male *abeona* and female *morrisi* and five reciprocal pairings; these gave me in the autumn of 1921 one hundred butterflies of the first generation. From these first generation specimens I secured ten further pairings, in no case mating brother and sister. The weather during the winter of 1921 was not at all conducive to success, and the larvae of the first generation had made such great inroads into the foodplant that I was only able in the spring of 1921 to secure thirty butterflies of the second generation. I made two successful pairings from these, which gave me twelve butterflies of the third generation in the autumn of 1922.

Fifteen of these butterflies have already been figured (28, pl. i.). They were chosen from the three generations, and also to parallel as far as possible the specimens of *joanna*, already figured in the Butterflies of Australia (29). It would be possible from amongst the specimens caught at Port Macquarie and the hybrids to secure even greater approximation.

Owing to the importance of this series of experiments a further set was begun in the spring of 1922, using, as before, butterflies of *abeona* from larvae and pupae obtained near Sydney, and of *morrisi* from larvae and pupae obtained at

Urunga. The experience obtained in the first set of experiments and the increase in the number of cages enabled me to secure, in the autumn of 1923, 126 butterflies of the first generation from 13 separate pairings. From pairings made amongst these first generation hybrids, I secured sixty-nine butterflies of the second generation. Having then over three hundred butterflies known to have resulted from the pairings of *abeona* and *morrisi*, I can say with confidence on comparing them with the specimens of the race *joanna* caught at Port Macquarie, that this race *joanna* is the result of such a crossing in nature. The experiments will be of added value when they are carried to a greater number of generations, for the equivalent of a first generation between *aurelia* and *morrisi* never occurs at Port Macquarie at the present day.

Previous to this, in 1919, I had made a pairing between a male *rawnsleyi* (emerged in Sydney, September 9) and obtained three males and two females as the result. Both these females were paired with brothers, and I secured seven specimens of the second generation. In October, 1919, I received freshly caught specimens of *rawnsleyi* from Mr. R. Illidge, one of which had laid an egg in its paper envelope; this emerged in 14 days and on March 3, 1920, produced a female. I at once secured a wild male and paired it, and in the spring of 1920 bred three males and a female.

In all I secured from these experiments 203 males and 177 females, including a large bulk experiment of several families placed in one cage, the male parents being *abeona* and the females *morrisi*.

The thorough examination of all these hybrids will necessarily be a long process, and for some of the points that require investigation, sufficient material has not yet been obtained to give accurate statistical results. Some points have been studied and are worthy of note.

The first series of experiments showed first generation families of 1 to 17 in the *abeona-morrisi* cross and families of 5 to 22 in the *morrisi-abeona* cross. In the second series the results were 2 to 12 for the *abeona-morrisi* cross and 5 to 23 for the *morrisi-abeona* cross. The average number of individuals per family for both series was eight for the *abeona-morrisi* cross and twelve for the *morrisi-abeona* cross. Thus when the mother was a specimen that emerged in its own locality, I secured an average of four more specimens than when the mother was reared from a larva brought to Sydney from a locality over 200 miles north.

When the whole of the male specimens of the two series of experiments were examined, I noticed that the males, whatever way the cross had been made, were all more or less similar and intermediate between *abeona* and *morrisi*. The band of the forewing above did not extend through the cell, but was always larger than that of *morrisi;* in colour it was never as deep as *abeona,* but more often was the colour of *morrisi*. The females, however, showed an interesting result. Whenever the male parent was the orange *abeona*, the resulting females always had orange markings, and if the male parent was *morrisi* the resulting females were white. This colouration of the wings following the male parent, also applied to those specimens which had a discal band on the hindwing above, as several of them had. This result was true for the 23 families, and also for the bulk experiment without exception.

The same applied to the two families in which *rawnsleyi* was used as one of the parents. With the *abeona-rawnsleyi* cross the female was orange, and with the *rawnsleyi-abeona* the two females were white. This goes a long way to prove that *rawnsleyi* is a race derived from *morrisi*, which has lost the white markings above.

The Explanation of the Origin of the Race joanna.

The explanation of the origin of this complex race *joanna* is dependent on the physiographical history of eastern Australia. At a period roughly dated as Pliocene (when Australia undoubtedly had a butterfly fauna) the shore stood farther eastwards than at present, trespassing upon what are now the Tasman and Coral Seas, the watershed was lower than at present and lay further westward, whilst the land continued south to Tasmania and beyond and north to New Guinea.

Then followed what Andrews has called the "Kosciusko Cycle," the coast retreated westwards, the coastal mountain range rose higher, Torres and Bass Strait opened. Movement of the coast range re-organised the river system and exposed different rocks to the surface. Specific differentiation in both fauna and flora then proceeded rapidly.

The palaeontological record shows so far no fossil butterflies earlier than the Tertiary, but in the Oligocene of both Europe and North America we find fossils of even the more developed groups and, included amongst these, several fossil Satyrids. Present-day Satyrids are of world-wide distribution, and there is every possibility that as early as the Miocene they had a similar distribution and that the ancestral forms of our present Bassian Satyrids were then in Australia.

It is reasonable to suppose that, before the great uplifting movement at the end of the Pliocene, the ancestor of *Tisiphone* was present in eastern Australia. I consider that first of all the genus became restricted to the higher elevations where moisture was more abundant. At the low-lying portion of the Main Divide known as the Cassilis Gap, the conditions became unsuited for its existence and it disappeared. This barrier then produced a discontinuous distribution and allowed the ancestral *Tisiphone* to develop independently to the north and to the south, gradually producing what we now know as broad orange banded forms in the south and narrow white banded forms in the north. The southern form now occurs almost up to the southern end of the Cassilis Gap and, though no form has been taken near the northern end of the Gap, a white banded form occurs at the southern end of the Mt. Royal Range almost in the same latitude. As time progressed the two forms were able to reach the coast, the southern probably first, and, finding suitable conditions, moved northward and southward, meeting in the small area of Port Macquarie and thus were able, in fairly recent times, to reunite and form the very complex race *joanna* there. Tasmania, though possessing the foodplant, does not possess any *Tisiphone*, which may possibly have died out or was not in a position to pass along the land connection at what is now Bass Straits. This would point to *Tisiphone* belonging rather to the earlier of the newer Papuan invasions from the north than to the older Satyrid fauna occurring in south-eastern Australia and now represented by such genera as *Heteronympha* and *Xenica*.

Summary and Conclusion.

The study of *Tisiphone abeona* illustrates an event that has not often been observed—the formation of no less than seven subspecies in a continental area. Subspecies more often arise as insular races, limited by definite barriers not liable to be broken, except at long intervals of time. Probably similar conditions exist nowhere else than in Australia. I know of no case nearly so marked amongst the *Rhopalocera*, the nearest approach being the four races of *Papilio priamus* occurring in tropical and subtropical parts of eastern Australia, but here the subspecific differences, though recognisable, are not very great. These butterflies belong to the rain forest, and the barriers that have caused their subspecific differ-

entiation have been the intervening dryer forest country. Where subspecific differences have been found in other Australian butterflies, the cause is not hard to discover. Many races of eastern species occur at Port Darwin, and some Tasmanian species differ slightly from the forms on the mainland. A few occur on the east coast, but none have their barrier anywhere near the latitude of the Cassilis Gap.

The ancestor of *abeona* entered Australia probably in early Pliocene times and advanced southwards to the present haunts of the species. Recent mountain building of the Kosciusko period changed both the local climate and the local physiography; *Tisiphone*, but not *Heteronympha*, responded to this change by branching off into a series of subspecies.

If we examine the range of some of the other Australian Satyrids in comparison with that of *T. abeona*, we find that *Heteronympha mirifica* is confined wholly within the range of the former, but I cannot find any tendency to subspecific differentiation, though six of the races of *abeona* occur in its range. Six races of *abeona* also occur in the range of *Heteronympha banksi*, but the latter species does not vary. *Heteronympha merope* occurs over the whole range of *abeona*, but, though two subspecies occur beyond its range, *H. merope* is particularly constant within the range of *abeona*. This points to *Tisiphone* being a much newer species than the constant species of *Heteronympha*.

It has been shown above that the four forms of *Tisiphone*, namely, *abeona*, *joanna*, *rawnsleyi*, and *morrisi*, which had for many years been considered distinct species, were not so, but only geographical races. They illustrate the process of evolution that had proceeded up to a certain point, when changes in the physiography of eastern Australia broke down the previous barrier at the Cassilis Gap and allowed the two distinct forms to mingle. Differentiation had not gone so far as to prevent these two from mating and having perfectly fertile offspring.

Had this barrier not been broken, an almost perfect example of species formation by isolation would have been presented to us.

Tisiphone shows an inclination to depart from two broods in a year to one brood. This change may be correlated with progress from a warmer to a cooler climate.

The explanation given of the origin of the hybrid race *joanna* hardly admits of any other view and suggests a very probable explanation of how new species may have arisen in some cases in the past.

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EXPLANATION OF PLATES.

Plate xxv.

Upper figure. Early stages of *Tisiphone abeona*. Egg much magnified, larva, larva pupating, lateral and dorsal views of pupa, all slightly magnified.

Lower figure. Early stages of *Oreixenica latialis*. 1. Egg much magnified. 2. Young larva magnified about 6 times. 3. Full grown larva magnified about 5 times. 4. Head of young larva much magnified. 5. Head of full grown larva much magnified. 6, 7,8. Lateral, dorsal and ventral views of pupa magnified about 5 times.

Plate xxvi.

I. *T. abeona regalis* n.subsp. Holotype male, Barrington Tops, February, 1925.

I.A. *T. abeona regalis* n.subsp. Paratype male, Barrington Tops, January 26, 1922.

II. *T. abeona regalis* n.subsp. Paratype female, Barrington Tops, emerged Sydney October 25, 1922.

II.A. *T. abeona regalis* n.subsp. Allotype female, Barrington Tops, January 26, 1922.

III. *T. abeona morrisi* Waterhouse, male, Urunga, emerged Sydney February 25, 1913.

III.A. *T. abeona morrisi* Waterhouse, male, Macksville, October 11, 1920.

IV. *T. abeona morrisi* Waterhouse,Paratype female, Ballina, October 11, 1902.

IV.A. *T. abeona morrisi* Waterhouse. Paratype female, Ballina, October 12, 1902.

(Figures I. and III. about 8/9 over natural size, figures II. and IV. slightly under natural size).